

# *The legacy of 20th Century landscape change on today's woodland carabid communities*

Article

Accepted Version

Neumann, J., Holloway, G. and Griffiths, G. (2017) The legacy of 20th Century landscape change on today's woodland carabid communities. *Diversity and Distributions*, 23 (12). pp. 1447-1458. ISSN 1472-4642 doi: <https://doi.org/10.1111/ddi.12652> Available at <https://centaur.reading.ac.uk/72222/>

It is advisable to refer to the publisher's version if you intend to cite from the work. See [Guidance on citing](#).

To link to this article DOI: <http://dx.doi.org/10.1111/ddi.12652>

Publisher: Wiley

All outputs in CentAUR are protected by Intellectual Property Rights law, including copyright law. Copyright and IPR is retained by the creators or other copyright holders. Terms and conditions for use of this material are defined in the [End User Agreement](#).

[www.reading.ac.uk/centaur](http://www.reading.ac.uk/centaur)

**CentAUR**

Central Archive at the University of Reading

Reading's research outputs online

**The legacy of 20<sup>th</sup> Century landscape change on today's woodland  
carabid communities**

Jessica L. Neumann<sup>1,2\*</sup>, Graham J. Holloway<sup>2</sup>, Andrew Hoodless<sup>3</sup> and Geoffrey H. Griffiths<sup>1</sup>

<sup>1</sup> *Department of Geography and Environmental Science, University of Reading, Reading, UK*

<sup>2</sup> *Centre for Wildlife Assessment and Conservation, School of Biological Sciences, University  
of Reading, Reading, UK*

<sup>3</sup> *Game and Wildlife Conservation Trust, Burgate Manor, Fordingbridge, Hampshire, UK*

**Author email addresses:** j.l.neumann@reading.ac.uk; g.j.holloway@reading.ac.uk;  
ahoodless@gwct.org.uk; g.h.griffiths@reading.ac.uk

**Keywords:** Carabidae, community analysis, extinction debt, landscape change, landscape  
heterogeneity, landscape mosaic

**Short running title:** Historical landscapes shape carabid communities today

**\*Corresponding author:** j.l.neumann@reading.ac.uk

Department of Geography and Environmental Science, University of Reading, Reading, UK

Tel: +44 (0)118 378 7285

**Abstract word count:** 300

**Main body word count:** 5209

**References:** 66

## 19 (A) ABSTRACT

### 20 Aim

21 For many species, the effects of landscape change can involve a time lag and result in an  
22 extinction debt. The landscape matrix plays a vital role in supporting species populations.  
23 However, the importance of the historical composition and configuration of landscape  
24 mosaics has received little attention, with studies focusing on the effects of loss and  
25 fragmentation of single (focal) habitat over time. We investigated the importance of historical  
26 and contemporary landscape heterogeneity (composition and configuration) to identify how  
27 landscape change has, and is continuing to have, an effect on current woodland carabid  
28 communities.

### 29 Location

30 Lowland Britain.

### 31 Methods

32 Carabids were sampled from woodlands in 36 tetrads of 4 km<sup>2</sup>. Ordination methods analysed  
33 current community response to representations of contemporary and historical (1930's)  
34 landscape heterogeneity. The effects of 80 years of landscape change on current carabid  
35 assemblages were compared among tetrads.

### 36 Results

37 Results are consistent with an extinction debt; carabid communities correlated significantly  
38 with the historical composition and configuration of the landscape, but not contemporary  
39 landscape configuration. Community assemblages have been shaped, and many species  
40 remain affiliated with landscape conditions that no longer exist, notably, large patches of

broadleaf woodland and semi-natural grassland. Recent introduction of conifer plantations has had a negative effect on the abundance of many woodland species. For many common, slow-dispersing species, contemporary and historical landscapes offered sub-optimum woodland coverage indicating a lag effect that exceeds 80 years. Increased arable landcover and loss of semi-natural grassland and heathland points towards an ongoing detrimental impact on carabid populations.

## **Main conclusions**

Compared with focal-habitat studies, the landscape mosaic approach provides a more comprehensive understanding of the effects of widespread landscape change on species communities. Conservation guidance includes new planting, maintenance and restoration of semi-natural habitats, implemented across multiple spatial scales and where feasible, considering both historical and contemporary landscape heterogeneity.

**(B) Keywords** Carabidae, community analysis, extinction debt, landscape change, landscape heterogeneity, landscape mosaic.

## (A) INTRODUCTION

Landscape change poses a serious threat to global biodiversity and there is concern regarding the loss of species in wooded-agricultural environments (Hendrickx *et al.*, 2007; Fahrig *et al.*, 2011). Over the last 80 years, agricultural intensification has led to widespread landscape modification across much of Europe, Australia and North America (Lunt & Spooner, 2005; Schweiger *et al.*, 2005). The loss and fragmentation of semi-natural habitats, plus transformation of land to intensive agriculture has fundamentally altered the compositional heterogeneity (the number and proportions of different landcover types) and configurational heterogeneity (the spatial arrangement of different landcover types) in the rural environment (Fahrig *et al.*, 2011). Changes to landscape heterogeneity alter the ecological filters which affect species-landscape processes such as dispersal, resource availability and colonisation (Mayfield *et al.*, 2010), ultimately influencing the abundance and diversity of species able to occupy habitats and exist in a landscape (Baessler & Klotz, 2006; Hendrickx *et al.*, 2007).

While some species respond almost immediately to landscape change, often there is a time lag effect (relaxation time), whereby species persist in a habitat, but the conditions they require for long-term survival are no longer being met fully; this is commonly referred to as an ‘extinction debt’ (Diamond, 1972; Tilman *et al.*, 1994). The present occupancy of species in a habitat patch may therefore, overestimate the carrying capacity of the current landscape and consequently, underestimate the threat to biodiversity even if no further landscape change occurs (Adriaens *et al.*, 2006; Piqueray *et al.*, 2011). Previous studies provide convincing evidence of extinction debts and lag effects across a range of habitats, taxa and spatial scales (see review by Kuussaari *et al.*, 2009). As such, a key issue in conservation biogeography is to identify how species respond to current landscape heterogeneity, but also to consider the temporal aspect. Ascertaining how species communities have been affected

and might continue to change in response to ongoing landscape change provides an indication of how biodiversity might respond to future conservation and land management decisions.

In temporal landscape research, a frequently adopted approach is to quantify and assess the interactions which exist between contemporary and past landscapes and current species distributions (e.g. Lindborg & Eriksson, 2004; Piessens & Hermy, 2006; Kuussaari *et al.*, 2009; Cristofoli *et al.*, 2010; Piqueray *et al.*, 2011; Husáková & Münzbergová, 2014). This approach reconstructs contemporary and past landscape configurations for a focal habitat of interest e.g., semi-natural grasslands (Sang *et al.*, 2010) or old-growth forest (Berglund & Jonsson, 2005). The presence of an extinction debt is inferred if the variation in current species richness, or the response of a functional group of species, is better explained by historical rather than contemporary landscape conditions. However, the binary classification of landscapes as either ‘focal habitat’, where resources required for the study taxa are met, or ‘hostile matrix’ (Fahrig *et al.*, 2011) means that conclusions regarding how species respond are solely based on contemporary and past configurations of one habitat type. It is however, known from studies that have analysed species response to current landscape conditions, that wider landscape heterogeneity is an important determinant of biodiversity (Haslem & Bennett, 2008; Duflot *et al.*, 2014; Neumann *et al.*, 2016). The ‘landscape mosaic’ approach, recognises that species are not only affected by the amount and spatial configuration of their focal habitat, but *also* by the composition of the heterogeneous matrix which can provide resources, alternative useable habitat and influence species dispersal (Fahrig *et al.*, 2011). In landscapes where focal habitat has been recently destroyed or fragmented, species might have dispersed into new patches, found alternative habitats in the matrix or, remained as an isolated population in the now compromised habitat patch. The past composition and configuration of the matrix is therefore, likely to be of significant explanatory importance for current species assemblages. Despite this, the effect of historical landscape composition has

received minimal attention (but see Lunt & Spooner, 2005; Baessler & Klotz, 2006; Aguirre-Gutiérrez *et al.*, 2015; Cousins *et al.*, 2015).

Post WWII in Britain, large areas of broadleaf woodland were cleared for intensive agriculture, fragmented by urban infrastructure, or converted to commercial coniferous plantations (Fuller *et al.*, 2007). This had a detrimental effect on woodland biodiversity (Hinsley *et al.*, 1995; Bellamy *et al.*, 1996; Mason, 2007). Landscape modification also occurred across other semi-natural habitats including species-rich grasslands and lowland heathland (Vickery *et al.*, 2001; Warren *et al.*, 2001). The alteration of landscape processes throughout the wider environment could potentially have affected species community assemblages in woodlands today.

This study investigated the response of woodland ground beetle communities (Coleoptera; Carabidae) to the contemporary and historical landscape heterogeneity (composition and configuration) of wooded-agricultural landscape mosaics in southern Britain (Fig. 1). Carabids were chosen as biological indicators as they are functionally diverse and sensitive to landscape change (Aviron *et al.*, 2005; Barbaro & van Halder, 2009). We analysed carabid response at the community level to include both specialist and generalist species, without restricting natural community variability or biasing carabid response by relying on specialists (Adriaens *et al.*, 2006). We asked, 1) do current woodland carabid communities exhibit a correlation with contemporary *and* historical landscapes when considering both the composition and configuration of landscape mosaics? 2) Is there evidence that current carabid distributions relate more strongly to representations of the historical landscape than the contemporary landscape, indicating a potential extinction debt? 3) Comparing results from contemporary and historical landscapes, is it possible to infer how landscape change might have had, or be having, an effect on current woodland carabid communities?



## (A) METHODS

### (B) *Study region*

The study was conducted in rural southern Britain (Fig. 1). The region is low-lying and temperate: average elevation 140 m a.s.l., mean annual temperature 10.2 °C, average annual precipitation 850 mm. In the 1930's prior to the onset of intensive agriculture, semi-natural habitats including species-rich meadows, grazing pastures, lowland heath and large patches of broadleaf woodland dominated the landscape. Arable land existed as small-scale plots used for non-intensive cropping, market gardens and orchards (Southall *et al.*, 2007). Today, the landscape is dominated by intensive arable farming (largely wheat, winter oil seed rape and barley) and improved grassland (for livestock, hay and silage production). Broadleaf woodland cover has been reduced into smaller, fragmented patches. Where larger woods have been retained, sizeable blocks have been converted to commercial coniferous plantations. Small areas of chalk downland, heathland and rough grassland exist as relict, isolated fragments (Fig. 1).

### (B) *Study design*

The study set-up follows previous research conducted by the authors in 2011. We refer readers to Neumann *et al.*, (2015) for a full detailed description of the methods. Thirty-six 2 x 2 km study tetrads were selected across the study region (Fig. 1); each was centred on a patch of broadleaf woodland, hereafter referred to as the sample woodland. Thirty of the sample woodlands were classified as Ancient Semi-Natural Woodland (Ancient Woodland Inventory – Natural England, 2013). The remaining six were continuously wooded for at least 165 years (County Series 1846-1969 maps – OS, 2013). Sample woodland size varied from 3 ha to 350 ha (median 51 ha). All were predominantly broadleaf although some larger woodlands contained stands of commercial coniferous plantation (Forestry Commission, 2013). The

composition of the landscape matrix within each tetrad was typical of the contemporary rural environment but tetrads differed in terms of their landscape configuration (i.e., amount, size, shape and arrangement of habitats). Tetrads contained uniform soil types, avoided areas of steep topography, large urban areas and coastal regions and did not overlap.

#### **(B) Contemporary map data**

Landcover Map 2007 (LCM2007) (Morton *et al.*, 2011) and Ordnance Survey MasterMap Topography data (OSMM) (OS, 2010) were used to quantify contemporary land-use. LCM2007 is an up-to-date UK land-use map representing the UK Biodiversity Action Plan Broad Habitats derived from 30 m resolution satellite imagery (NERC, 2011). The spatial and thematic accuracy of LCM2007 when validated against ground reference data was 83% and the minimum mappable area was 0.5 ha meaning small or complex-shaped features e.g., small water bodies, are not well represented (NERC, 2011). To overcome these inaccuracies the LCM2007 data were combined with the OSMM Topography data. OSMM details landscape features (e.g. buildings, roads, woodlands, water bodies) as individual polygons with 2.5 – 6.0 m spatial accuracy in rural areas but does not specify definitive landcover information (OS, 2010). For each tetrad, a comprehensive landcover dataset was created in ArcMap 10.1 (ESRI, 2011) using information from both datasets.

#### **(B) Historical map data**

The first systematic survey of land in Great Britain was carried out under the direction of Professor Dudley Stamp in the early 1930's (Hooftman & Bullock, 2012). The Dudley Stamp Maps (DSM) categorised land-use at the one-inch-to-the-mile (1:63,360) scale and were printed between 1933 and 1949. Digitisation of the original paper maps was completed in 2011 (Clark, 2011). DSM maps seven Broad Habitats: (i) forest and woodland; (ii)

176 meadowland and permanent grasslands; (iii) arable land; (iv) water; (v) heath and moorland;  
177 (vi) urban core; (vii) suburban (gardens etc.) (Southall *et al.*, 2007).

178 ***(B) Landscape heterogeneity spatial analysis***

179 ArcMap 10.1 was used to quantify the contemporary and historical landscape heterogeneity  
180 (landscape composition and configuration) within each tetrad (Table 1). To facilitate  
181 comparisons between current and past landscapes, the contemporary LCM2007 data were  
182 classified to be comparable with the Broad Habitats represented in the DSM (see Table S1,  
183 Supporting Information).

184 ***(C) Landscape composition***

185 Contemporary landscape composition in each tetrad was represented by the relative  
186 proportion of the eight Broad Habitat variables. Six were used to characterize the historical  
187 landscape composition; improved grassland and coniferous plantation were not present  
188 historically (Table 1).

189 ***(C) Landscape configuration***

190 Landscape configuration metrics measured the number, amount, shape and spatial  
191 configuration of the Broad Habitat variables in each tetrad (Table 1). Discrete habitat patches  
192 had an edge-to-edge Euclidean distance of at least 20 m from another patch of the same type.  
193 Functionally, 20 m exceeds the ‘interaction distance’ for many common carabid species  
194 (Brouwers & Newton, 2009). The number of patches and mean patch area indicated the  
195 degree of structural fragmentation of a Broad Habitat type (Cristofoli *et al.*, 2010).

196 ***(C) Additional constraining variables***

The detection of true landscape effects on communities can be hampered by constraining variables (Table 1). For all analyses, the effects of carabid sampling date and spatial autocorrelation (where tetrads in close proximity to each other can possess more similar landscape or biotic conditions than those from a random set of observations) were accounted for (see below) (Heikkinen *et al.*, 2004; Oliver *et al.*, 2010).

### **(B) Sampling carabid communities**

Carabid communities in each sample woodland were surveyed using 10 pitfall traps set between May and early August 2011. Two pitfall traps were placed at the centre of each sample woodland. Further pairs were set along the most northerly, southerly, easterly and westerly facing-woodland edge adjacent with the non-woodland habitat. Pitfall traps (diameter 60 mm, depth 80 mm) were one third filled with ethylene glycol (50%) and water (50%). In each tetrad, traps were set continuously for 14 days, randomly assigned between May and August to avoid clusters of tetrads in close proximity trapping species over the same time period. Individuals collected were pooled for each tetrad and identified to species using Luff (2007).

### **(B) Statistical analyses**

The effects of contemporary and historical landscape heterogeneity on current woodland carabid communities were explored using partial canonical correspondence analyses (pCCA) in Canoco 5 (ter Braak & Šmilauer, 2012). Analyses followed a two-step process: 1) global permutation tests 2) interactive forward selection procedure. Partial methods were used in all tests to account for, and remove any variation explained by ‘sampling date’. The effect of spatial autocorrelation was addressed using principal coordinates of neighbour matrices (PCNM) (see Borcard & Legendre, 2002).

220 Four pCCA models were run; one each testing for an effect of landscape composition or  
 221 landscape configuration in both contemporary and historical landscapes on woodland carabid  
 222 communities. For each model, a constrained ordination containing all the explanatory  
 223 variables (Table 1) was run to check for significance of the joint effects; a global permutation  
 224 test was considered significant where  $p < 0.05$  using 9999 Monte-Carlo permutations. The  
 225 Monte-Carlo test repeatedly shuffled the species data while keeping the explanatory  
 226 landscape variables (and 'sampling date' covariate) fixed to identify any biologically  
 227 plausible structure in the data. Following a significant result, partial interactive forward  
 228 selection (pIFS) was used to reduce the whole set of variables to a more parsimonious subset  
 229 that explained a good proportion of the constrained variation in the carabid community  
 230 composition. At each step, the landscape variable that added most to the explained  
 231 community composition variation was selected (in addition to the effects of explanatory  
 232 variables that had already been selected). The statistical significance of each variable was  
 233 determined using Monte-Carlo permutations. The results of pIFS were displayed as bi-plots  
 234 illustrating the 25 most important carabid species relationships with the selected landscape  
 235 variables. On the bi-plots, arrows representing landscape variables point in the direction of  
 236 the steepest increase in a variables value. Symbols representing beetle species can be  
 237 perpendicularly projected onto the landscape variable line using a calibration arrow in the  
 238 Canoco software to determine the optima of an individual species in respect to the value of  
 239 that landscape variable. This interpretation is underpinned by some assumptions (see  
 240 Legendre and Legendre, 1998), notably that species have a unimodal relationship of (log-  
 241 transformed) abundance with the landscape variable and that the landscape gradient is long  
 242 enough to allow a species to go from a sub-optimum low frequency and on to a level of past-  
 243 optimum lower frequency. Nonetheless, use of the calibration arrow provides a useful  
 244 indication of *approximated* species response, whereby 'optimum' represents the value of the

environmental variable in the study at which a species is predicted to have its highest (log) abundance.

Multicollinearity between explanatory variables is common in study tetrads where landcover composition sums to 1 (Heikkinen *et al.*, 2004). The landscape composition variables (Table 1) were log (x+1) transformed to maximise the linearity of their relation to each other and to ensure that the ecological importance of all the landcover types for species was considered (Cleveland, 1993; ter Braak & Šmilauer, 2012). In all cases, the correlation matrix and variance inflation factors were consulted during the Global Permutation Test to check for collinearity (ter Braak & Šmilauer, 2012). Correlation coefficients among the final explanatory variables were all less than 0.6 (Table S2) (cf. Aviron *et al.*, 2005, Radford & Bennett, 2007). The full matrix of carabid species were log (x+1) transformed to minimize the impact of abundant species on the analyses (Vanbergen *et al.*, 2005).

## **(A) RESULTS**

### ***(B) Land-use change***

Land-use changes are summarised in Table 2. Historically, study tetrads were dominated by semi-natural grasslands and broadleaf woodland. Approximately 25% of the landscape was used for arable production and 8% lowland heath and scrubland. Today, grasslands represented 3.6% of tetrad landcover; a relative decline of 91%. Grassland patches almost halved in number and decreased substantially in size. Lowland heath and scrub habitat underwent a relative loss of 95%. The majority of grassland and heathland habitat was converted to improved grassland and intensive arable land-use, together representing the largest proportion of landcover in the contemporary landscape (combined average 241.6 ha or 60.4%).

268 Broadleaf woodland habitat declined by 10 ha on average; a loss of 2.4%. Despite a relatively  
269 low level of loss, contemporary woodlands now exist as substantially smaller, more  
270 numerous patches with increased woodland edge habitat. Coniferous plantations were not  
271 present historically, but represented 14.2 ha (3.5%) of tetrad landcover today. Total woodland  
272 habitat inclusive of coniferous plantations increased by 1.1%. Urban land-use and transport  
273 infrastructure also increased over the 80 years.

274 Table S2 shows variable collinearity between different years. Variables of the same habitat  
275 type showed moderate to strong positive correlations over time; broadleaf woodland ( $r =$   
276 0.63), urban ( $r = 0.65$ ), inland water ( $r = 0.67$ ) and road length ( $r = 0.79$ ). Pairwise  
277 comparisons indicated moderate positive correlation between historical semi-natural  
278 grassland and contemporary improved grassland cover ( $r = 0.56$ ) and historical heathland and  
279 contemporary coniferous woodland cover ( $r = 0.45$ ).

## 280 **(B) *Carabid* community dynamics**

281 4677 carabid beetles comprising 76 species were recorded from the 36 tetrads. 80% were  
282 from five widespread woodland and generalist habitat species: *Pterostichus madidus* (1809,  
283 39% of the total), *Abax parallelepipedus* (1354, 29%), *Pterostichus melanarius* (303, 6%),  
284 *Nebria brevicollis* (162, 3%) and *Calathus rotundicollis* (155, 3%). Other species recorded  
285 frequently but in lower abundances included grassland, open habitat, agricultural and  
286 heathland species (Table S3).

## 287 **(B) *Effect of spatial autocorrelation***

288 Principal coordinates of neighbouring matrices (PCNM) found no spatially conditioned  
289 variation in the contemporary landscape composition or configuration variables ( $p = 0.289$

and  $p = 0.740$ ), nor the historical composition or configuration variables ( $p = 0.326$  and  $p = 0.540$ ) which could explain the carabid community composition.

**(B) Carabid community response to contemporary and historical landscape heterogeneity**

**(C) Contemporary landscape composition**

Woodland carabid community composition was significantly related to contemporary landscape composition (pCCA,  $F = 1.3$ ,  $p = 0.009$ ); the eight landscape composition variables explained 29.7% of the total community variation (Table 3; Fig. 2). pIFS selected four Broad Habitat variables that accounted for 18.0% of the total variation in carabid communities (Fig. 2). Species recorded less frequently during the study exhibited the strongest response; *C. rotundicollis* (C.rot) was the only one of the five commonly trapped species to appear on the bi-plot (Fig. 2). Most species associated negatively with contemporary expanses of arable land and coniferous plantation which respectively explained 4.9% ( $p = 0.015$ ) and 3.9% ( $p = 0.098$ ) of the total variation (Table 3; Fig. 2). Species associated with mature broadleaf woodlands including *Bembidion mannerheimii* (B.man), *Calodromius spilotus* (C.spi) and *Acupalpus dubius* (A.dub) were among those to respond most negatively to these two variables. Only heathland specialist *Nebria salina* (N.sal) and generalist woodland species *C. rotundicollis* (C.rot) had their highest relative (log) abundances in landscapes containing 35 – 40% arable landcover and 3 – 6% coniferous plantation; values typical of the contemporary landscape (Table 1; Fig. 2). *Notiophilus quadripunctatus* (N.qua), *Amara ovata* (A.ova) and *Paranchus albipes* (P.alp) were most abundant in tetrads containing 3 – 4% semi-natural grassland (mean cover 3.6%; Table 2, Fig. 2).

**(C) Historical landscape composition**



Woodland carabid community composition was significantly related to the historical landscape composition (pCCA,  $F = 1.3$ ,  $p = 0.005$ ); the six variables explained 23.0% of the total community variation (Table 3). Arable land ( $p = 0.008$ ) and broadleaf woodland ( $p = 0.031$ ) accounted for 10.2% of the total variation during pIFS (Table 3, Fig. 3). Thirteen of the 25 species represented on the bi-plot responded to both the contemporary and historical landscape composition (Figs. 2 and 3). However, with the exception of arable land, the two models identified different explanatory landscape variables as key determinants of community composition. Many species continued to display negative associations with historical levels of arable land (Fig. 3). With the exception of *Calathus fuscipes* (C.fus) (an inhabitant of arable fields) all other species represented on the bi-plot appeared at greater abundance in tetrads with a proportion of arable land below that of the historical average (23.5%). The approximate amount of broadleaf woodland cover that maximized the predicted abundance of all species represented (other than agricultural species *Synuchus vivalis* (S.viv) and *Bembidion quadrimaculatum* (B.qua)) was slightly greater than the historical average of 26.6% (Table 2, Fig. 3). *Pterostichus niger* (P.nig) (a large-bodied (18.5 mm), flightless inhabitant of woodlands and damp grasslands) and *Carabus problematicus* (C.pro) (a very large (24 mm), flightless inhabitant of woodland and heathland) were recorded in over two-thirds of the study tetrads, but correlated only with historical landscape composition (Fig. 3).

### (C) Contemporary landscape configuration

Woodland carabid communities exhibited a near-significant response to contemporary landscape configuration when testing the joint effects (pCCA;  $F = 1.3$ ,  $p = 0.064$ ). The 9 configuration variables explained 32.1% of the total variation. Length of woodland edge and mean woodland patch area explained the greatest proportion of the variation; 4.8% ( $p = 0.033$ ) and 4.2% ( $p = 0.084$ ) respectively (Table 3, Fig. 4). Grassland, heathland and open-habitat species were most prevalent on the bi-plot. Those located in the positive bi-plot

quadrant (top-right) had highest predicted abundance where woodland edge exceeded 22 km (contemporary mean 19.8 km). Woodland species including *Bembidion aeneum* (B.aen) and specialist *Leistus fulvibarbis* (L.ful) were most abundant where landscapes contained large woodland patches (~12 ha).

### (C) Historical landscape configuration

Variation in current woodland carabid communities was better explained by historical landscape configuration than contemporary landscape configuration when testing the joint effects (pCCA:  $F = 1.4$ ,  $p = 0.006$ , 34.7%) (Table 3). Four historical configuration variables explained 17.7% of the total variation (Table 3, Fig. 5). Historically larger patches of broadleaf woodland ( $p = 0.062$ ) and semi-natural grassland ( $p = 0.064$ ) explained the greatest amount of carabid community variation (Table 3, Fig. 5). These two Broad Habitat types also contributed to the largest proportions of total historical landcover (Table 2). *C. rotundicollis* (C.rot), *A. parallelepipedus* (A.par) and *P. melanarius* (P.mel), three of the five most frequently trapped species, were optimally associated with landscapes containing 0.2 – 0.6 km of transport routes (historical average of 1.8 km) (Table 2). In addition to *C. problematicus* (C.pro) these common and widespread woodland species were found in greater abundance in tetrads with 10 – 11.5 km of woodland edge habitat (historical average 11.3 km) and woodland patches sized 16 – 26 ha (historical average 16.3 ha). Woodland species *B. mannerheimii* (B.man), *C. spilotus* (C.spi) and *A. dubius* (A.dub) positively associated with historically large patches (> 28 ha) of broadleaf woodland (Fig. 5). *N. quadripunctatus* (N.qua), *A. ovata* (A.ova) and *P. albipes* (P.alb) correlated strongly with landscapes that historically contained grassland patches larger than 60 ha (historical average 36.7 ha) (Table 2, Fig. 5).

### (A) DISCUSSION

Recently, it has become more widely accepted that species perceive landscapes in a complex manner and utilise resources from different landcover types beyond their focal habitat (Haslem & Bennett, 2008; Oliver *et al.*, 2010; Fahrig *et al.*, 2011). It has also been demonstrated that the response of many species to landscape change is typically not instant, but involves a time lag (Diamond, 1972). It was therefore, anticipated that populations would exhibit a response to a variety of habitats present in the contemporary landscape, but also those representative of the historical landscape (Kuussaari *et al.*, 2009; Watts *et al.*, 2010).

***(B) Evidence of extinction debt for carabid communities in wooded-agricultural landscapes***

Carabid communities correlated significantly with both contemporary and historical landscape composition, although more of the variation was explained by the contemporary landscape. However, the significant effect of historical landscape composition is indicative that some species may be experiencing a lag effect i.e., persisting as a result of landscape conditions which no longer exist placing them at heightened risk of future extinction (Lindborg & Eriksson, 2004). By contrast, the significant response of current carabid communities to historical but not contemporary landscape configuration is consistent with an extinction debt (Lindborg & Eriksson, 2004; Berglund & Jonsson, 2005; Sang *et al.*, 2010).

In the landscape composition models, 13 of the same species represented on the bi-plots responded to both contemporary and historical conditions yet, apart from arable land, different explanatory variables were identified. This is strong evidence that past habitat availability is a key factor explaining current community assemblages (Sang *et al.*, 2010), and also indicates that many of the same species are continuing to react to different, altered conditions in the contemporary landscape. The negative association of many species to historical amounts of arable land and positive relationship with historical availability of

broadleaf woodland is not unexpected as species will often respond most strongly to the extent of preferred or avoided elements in a landscape (Judas *et al.*, 2002; Heikkinen *et al.*, 2004; Aviron *et al.*, 2005). Indeed, the approach adopted in other temporal landscape studies assumes that species will correlate significantly with representations of their focal habitat. However, in this study, the same species did not yield a response to contemporary broadleaf woodland cover, despite only declining by 2.4% over the 80 years and with a moderately strong correlation between years (i.e., tetrads with greater woodland cover historically retained greater amounts of woodland today (Table S2)). What was observed was a continued negative association to the vast increase in arable land cover, and also to coniferous plantations which were not present historically. In lowland Britain, most conifer plantations are sited on heathland (Spencer & Haworth, 2005) (which showed moderate correlation between years), and within large patches of broadleaf, often ancient semi-natural woodland (Rackham, 2003; Natural England, 2013). The strong negative association with conifers was most evident for species typical or specialist of mature woodland including *B. mannerheimii*, *C. spilotus* and *A. dubius*; these species also optimally associated with large patches of broadleaf woodland in the historical model. The ongoing impacts of woodland conversion are likely to continue to be detrimental as abundance and richness measures within introduced coniferous plantations have consistently been found to be lower than those associated with mature broadleaf woodland (Wiezik *et al.*, 2007; Oxborough *et al.*, 2010). Contrarily, there is evidence that heathland soil structure and fertility is less altered by plantations, helping to support heathland specialists such as *N. salina* and offering potential areas for conservation restoration focus (Spencer & Haworth, 2005).

In the landscape configuration models, carabid communities were most strongly associated with historically large patches of broadleaf woodland and semi-natural grasslands. These two habitats contributed to the largest proportion of historical landcover, again indicating a legacy

whereby current woodland carabid assemblages have been shaped, and remain affiliated to features which were dominant 80 years ago. The continued prevalence of *N. quadripunctatus*, *A. ovata* and *P. albipes* (open/grassland habitat species) in landscapes that retain just 3 – 4% grassland cover today, suggests that some species may only persist if landscape conditions were exceptionally favourable previously, i.e., the highest abundance of these species was in tetrads that historically included grassland patches larger than 60 ha (average historical patch size 36.7 ha). Further studies adopting the temporal landscape mosaic approach but sampling within grassland habitats would help confirm this assumption.

The degree of habitat fragmentation within a landscape has been found to be of significant importance when it comes to identifying extinction debts (e.g. Cousins, 2009; Cristofoli *et al.*, 2010; Piqueray *et al.*, 2011; Rybicki & Hanski, 2013). Here, the break-up of woodland into smaller, more numerous patches, leading to an increase in edge habitat but with little loss in total woodland cover is indicative of fragmentation. Evidence from the contemporary configuration model however, suggested that the effect on species was not uniform: larger patches may be key for specialists like *L. fulvibarbis*, while greater amounts of woodland edge appeared to benefit other grassland, heathland and open-habitat species; possibly by acting as a buffer, providing alternative useable or refuge habitat following substantial semi-natural habitat loss (Schweiger *et al.*, 2005; Hendrickx *et al.*, 2007; Neumann *et al.*, 2015).

This highlights the need for a landscape mosaic approach that ensures the values of other landcover types are not ignored. Likewise, although a negative effect of fragmentation was not conclusive, it must be noted that focal habitat studies focussing on the response of specialists are more likely to observe a significant effect as species will express higher sensitivity to changes in their specific habitat, particularly in the absence of other landcover information (Sang *et al.*, 2010). Nonetheless, there is increasing recognition that landscape change impacts on the process of community assembly (Mayfield *et al.*, 2010) and that the

response of generalists are equally important to fully understand the ongoing impacts on community structure (Cousins & Vanhoenacker, 2011; Piqueray *et al.*, 2011).

***(B) How might landscape change be having an effect on carabid communities?***

This, and previous studies (e.g. Barbaro & Van Halder, 2009; Sang *et al.*, 2010; Duflot *et al.*, 2014; Neumann *et al.*, 2015) indicate that specialists and carabids with lower dispersal ability may be at greater risk following landcover change. In this study, large-bodied and flightless carabids including *P. niger*, *C. problematicus*, *A. parallelepipedus* and *P. melanarius* responded only to historical landscape conditions. All however, are considered common and widespread (Luff, 2007) and were identified from more than two-thirds of the woodlands sampled. The dispersal of large-bodied, flightless, carabids takes several generations and successful colonisation of new patches may take hundreds of years (Jopp & Reuter, 2005). Their frequency today should not be assumed to represent a stable and healthy population, but may be better viewed as *persisting* (Oliver *et al.*, 2010) and in need of appropriate targeted land management actions. Indeed, the relative abundance of these species was greatest where the extent, shape and size of broadleaf woodland habitat was found to be greater than, or at the threshold of that provided in the landscape 80 years ago. Although a pertinent issue currently, the loss of woodland habitat in Britain can be dated back to the Neolithic (Rackham, 1986) suggesting that, for many species, the extinction debt currently being paid may relate to landscape conditions present well beyond the time period considered here.

***(B) Value of the landscape mosaic approach***

The landscape mosaic approach allows simultaneous consideration of landscape composition and configuration as complementary components. Until now, temporal landscape studies have only considered changes in the configuration of focal habitat (e.g. Lindborg & Eriksson,

2004; Cristofoli *et al.*, 2010; Sang *et al.*, 2010; Husáková & Münzbergová, 2014), which may overemphasise the effects of landscape change on biodiversity. In this study, the landscape mosaic approach stressed the importance of historical landscape conditions, but also highlighted which habitats in the modified environment served to bolster populations and those which were detrimental, providing a better understanding of how community assemblages have been, and may continue to be shaped.

### **(B) Conservation implications**

The detection of an extinction debt provides an unknown deadline for future biodiversity loss, however, while species persist, there remains time for conservation measures to be applied. Lowland Britain will remain dominated by intensive agriculture for the foreseeable, thus a combination of management approaches are needed. For species with low dispersal power, maintaining or increasing the size of woodland patches is advocated, while facilitating species movement through the introduction and maintenance of linear features is a recognised option where intensive agriculture dominates the landscape (Lawton *et al.*, 2010; Watts *et al.*, 2010). There is good evidence that species-rich hedgerows also offer comparable conditions to woodland edges (Taboada *et al.*, 2004), which if providing refuge habitat for species of open-habitats will ensure that linear features provide co-benefits throughout the matrix. Active conversion of plantation woodland back to native tree species or heathland is recognised (Spencer & Haworth, 2005) and guidance might consider restoration or new woodland planting to be conducted at a level equivalent to the amount of habitat lost to plantation. Restoration of heathland and species-rich grassland must be encouraged where feasible (Piessens & Hermy, 2006) especially smaller patches implemented under farm-level stewardship that connect larger restoration efforts. Finally, conservation actions should consider the composition and configuration of both the historical and contemporary landscape to ensure that efforts are applied where they are most suitable, encouraging

maximum biodiversity gain. For example, semi-natural grassland restoration might be best undertaken on nutrient-depleted ex-arable land that retains a history of being on (or near to) previous grassland sites to assist the development of species-rich swards (Walker *et al.*, 2004). While such strategic conservation planning ideally requires access to historical spatial data, local knowledge will be invaluable where spatial datasets are unavailable.

#### (A) ACKNOWLEDGEMENTS

We are grateful to Chris Foster for his help with data collection and to landowners who granted us access to their land.

#### (A) REFERENCES

- Adriaens, D., Honnay, O. & Hermy, M. (2006) No evidence of a plant extinction debt in highly fragmented calcareous grasslands in Belgium. *Biological Conservation*, **133**, 212–224.
- Aguirre-Gutiérrez, J., Biesmeijer, J.C., van Loon, E.E., Reemer, M., WallisDeVries, M.F. & Carvalheiro, L.G. (2015) Susceptibility of pollinators to ongoing landscape changes depends on landscape history. *Diversity and Distributions*, **21**, 1129–1140.
- Aviron, S., Burel, F., Baudry, J. & Schermann, N. (2005) Carabid assemblages in agricultural landscapes: impacts of habitat features, landscape context at different spatial scales and farming intensity. *Agriculture, Ecosystems and Environment*, **108**, 205–217.
- Baessler, C. & Klotz, S. (2006) Effects of changes in agricultural land-use on landscape structure and arable weed vegetation over the last 50 years. *Agriculture, Ecosystems and Environment*, **115**, 43–50.



506 Barbaro, L. & van Halder, I. (2009) Linking bird, carabid beetle and butterfly life history  
 507 traits to habitat fragmentation in mosaic landscapes. *Ecography*, **32**, 321–333.

508 Bellamy, P., Hinsley, S.A. & Newton, I. (1996) Factors influencing bird species numbers in  
 509 small woods in South-East England. *Journal of Applied Ecology*, **33**, 249–262.

510 Berglund, H. & Jonsson, B.G. (2005) Verifying an extinction debt among lichens and fungi  
 511 in Northern Swedish boreal forests. *Conservation Biology*, **19**, 338–348.

512 Borcard, D. & Legendre, P. (2002) All-scale spatial analysis of ecological data by means of  
 513 principal coordinates of neighbour matrices. *Ecological Modelling*, **153**, 51–68.

514 Brouwers, N. & Newton, A.C. (2009) Movement rates of woodland invertebrates: a  
 515 systematic review of empirical evidence. *Insect Conservation & Diversity*, **2**, 10–22.

516 Clark, A.N. (2011) Data from: The Land Utilisation Survey of Britain, 1933-1949  
 517 (unpublished). Coverage: Great Britain. Environment Agency and obtained under Special  
 518 Non-Commercial licence. Available at: [http://data.gov.uk/dataset/digital-land-utilisation-](http://data.gov.uk/dataset/digital-land-utilisation-survey-1933-1949-afa213)  
 519 [survey-1933-1949-afa213](http://data.gov.uk/dataset/digital-land-utilisation-survey-1933-1949-afa213).

520 Cleveland, W.S. (1993) *Visualizing data*. Hobart Press, New Jersey.

521 Cousins, S.A.O. (2009) Extinction debt in fragmented grasslands: paid or not? *Journal of*  
 522 *Vegetation Science*, **20**, 3–7.

523 Cousins, S.O. & Vanhoenacker, D. (2011) Detection of extinction debt depends on scale and  
 524 specialisation. *Biological Conservation*, **144**, 782–787.

525 Cousins, S.O., Auffret, A.G., Lindgren, J. & Tränk, L. (2015) Regional-scale land-cover  
 526 change during the 20th century and its consequences for biodiversity. *Ambio*, **44**, 17-27.

527 Cristofoli, S., Monty, A. & Mahy, G. (2010) Historical landscape structure affects plant  
 528 species richness in wet heathlands with complex landscape dynamics. *Landscape and Urban*  
 529 *Planning*, **98**, 92–98.

530 Diamond, J.M. (1972) Biogeographic Kinetics: Estimation of Relaxation Times for  
 531 Avifaunas of Southwest Pacific Islands. *Proceedings of the National Academy of Science*  
 532 *USA*, **69**, 3199–3203.

533 Dufлот, R., Georges, R., Ernoult, A., Aviron, S. & Burel, F. (2014) Landscape heterogeneity  
 534 as an ecological filter of species traits. *Acta Oecologia*, **56**, 19–26.

535 ESRI. (2011) ArcGIS Desktop: Release 10. Redlands, CA: Environmental Systems Research  
 536 Institute.

537 Fahrig, L., Baudry, J., Brotons, L., Burel, F.G., Crist, T.O., Fuller, R.J. Sirami, C.,  
 538 Siriwardena, G. & Martin, J-L. (2011) Functional landscape heterogeneity and animal  
 539 biodiversity in agricultural landscapes. *Ecology Letters*, **14**, 101–112.

540 Forestry Commission (2013) Data from: National Forest Inventory Great Britain 2013.  
 541 Forestry Commission. Data obtained under Ordnance Survey Open Data terms. Available at:  
 542 <http://www.forestry.gov.uk/forestry/infd-8g5bx3>.

543 Fuller, R.J., Smith, K.W., Grice, P.V., Currie, F.A. & Quine, C.P. (2007) Habitat Change and  
 544 Woodland Birds in Britain: Implications for management and future research. *Ibis*, **149**, 261–  
 545 268.

546 Haslem, A. & Bennett, A.F. (2008) Birds in Agricultural Mosaics: The Influence of  
 547 Landscape Pattern and Countryside Heterogeneity. *Ecological Applications*, **18**, 185–196.

548 Heikkinen, R.K., Luoto, M., Virkkala, R. & Rainio, K. (2004) Effects of habitat cover,  
 549 landscape structure and spatial variables on the abundance of birds in an agricultural forest  
 550 mosaic. *Journal of Applied Ecology*, **41**, 824–835.

551 Hendrickx, F., Maelfait, J., Van Wingerden, W., Schweiger, O., Speelmans, M., Aviron, S.,  
 552 Augenstein, I., Billeter, R., Bailey, D., Bukacek, R., Burel, F., Diekotter, T., Dirksen, J.,  
 553 Herzog, F., Liira, J., Roubalova, M., Vandomme, V. & Bugter, R. (2007) How landscape  
 554 structure, land-use intensity and habitat diversity affect components of total arthropod  
 555 diversity in agricultural landscapes. *Journal of Applied Ecology*, **44**, 340–351.

556 Hinsley, S.A. & Bellamy, P.E. (2000) The influence of hedge structure, management and  
 557 landscape context on the value of hedgerows to birds: a review. *Journal of Environmental*  
 558 *Management*, **80**, 33–49.

559 Hinsley, S.A., Bellamy, P.E. & Newton, I. (1995) Bird Species Turnover and Stochastic  
 560 Extinction in Woodland Fragments. *Ecography*, **18**, 41–50.

561 Hooftman, D.A.P. & Bullock, J.M. (2012) Mapping to inform conservation: A case study of  
 562 changes in semi-natural habitats and their connectivity over 70 years. *Biological*  
 563 *Conservation*, **145**, 30–38.

564 Husáková, I. & Münzbergová, Z. (2014) Relative importance of current and past landscape  
 565 structure and local habitat conditions for plant species richness in dry grassland-like forest  
 566 openings. *PLoS ONE*, **9**, p.e97110 (online).

567 Jopp, F. & Reuter, H. (2005) Dispersal of carabid beetles – emergence of distribution  
 568 patterns. *Ecological Modelling*, **186**, 389–405.

569 Judas, M., Dornieden, K. & Strothmann, U. (2002) Distribution patterns of carabid beetle  
 570 species at the landscape-level. *Journal of Biogeography*, **29**, 491–508.

571 Kuussaari, M., Bommarco, R., Heikkinen, R.K., Helm, A., Krauss, J., Lindborg, R.,  
 572 Ockinger, E., Partel, M., Pino, J., Roda, F., Stefanescu, C., Teder, T., Zobel, M. & Steffan-  
 573 Dewenter, I. (2009) Extinction debt: a challenge for biodiversity conservation. *Trends in*  
 574 *Ecology & Evolution*, **24**, 564–571.

575 Lawton, J.H., Brotherton, P.N.M., Brown, V.K., Elphick, C., Fitter, A.H., Forshaw, J.,  
 576 Haddow, R.W., Hilborne, S., Leafe, R.N., Mace, G.M., Southgate, M.P., Sutherland, W.J.,  
 577 Tew, T.E., Varley, J. & Wynne, G.R. (2010) *Making Space for Nature: a review of England's*  
 578 *wildlife sites and ecological network*. Report to Defra.

579 Legendre, P. & Legendre, L. (1998) *Numerical Ecology*. 2<sup>nd</sup> Edition, Elsevier Science,  
 580 Amsterdam, Netherlands.

581 Lindborg, R. & Eriksson, O. (2004) Historical landscape connectivity affects present plant  
 582 species diversity. *Ecology*, **85**, 1840–1845.

583 Luff, M.L. (2007) *The Carabidae (ground beetles) of Britain and Ireland*. FSC Publications,  
 584 Shrewsbury, UK.

585 Lunt, I.D. & Spooner, P.G. (2005) Using historical ecology to understand patterns of  
 586 biodiversity in fragmented agricultural landscapes. *Journal of Biogeography*, **32**, 1859–1873.

587 Mason, W.L. (2007) Changes in the management of British forests between 1945 and 2000  
 588 and possible future trends. *Ibis*, **149**, 41–52.

589 Mayfield, M., Bonser, S.P., Morgan, J., Aubin, I., McNamara, S. & Vesk, P.A. (2010) What  
 590 does species richness tell us about functional trait diversity? Predictions and evidence for  
 591 responses of species and functional trait diversity to land-use change. *Global Ecology and*  
 592 *Biogeography*, **19**, 423–431.

593 Morton, D., Rowland, C., Wood, C. & Meek, L. (2011) *Final Report for LCM2007 - the new*  
594 *UK Land Cover Map*. Countryside Survey Technical Report No 11/07. Natural Environment  
595 Research Council (NERC). Centre for Ecology and Hydrology (CEH), UK.

596 Natural England. (2013) Download Environmental Data: Ancient Woodlands. Coverage:  
597 Great Britain. Obtained under non-commercial licence. Available at:  
598 [http://www.geostore.com/environment-agency/WebStore?xml=environment-](http://www.geostore.com/environment-agency/WebStore?xml=environment-agency/xml/ogcDataDownload.xml)  
599 [agency/xml/ogcDataDownload.xml](http://www.geostore.com/environment-agency/WebStore?xml=environment-agency/xml/ogcDataDownload.xml)

600 NERC. (2011) *Landcover Map 2007 Dataset documentation*. Version 1.0. Natural  
601 Environment Research Council. Oxfordshire: Centre for Ecology and Hydrology (CEH).

602 Neumann, J.L., Griffiths, G.H., Hoodless, A. & Holloway, G.J. (2015) The compositional  
603 and configurational heterogeneity of matrix habitats shape woodland carabid communities in  
604 wooded-agricultural landscapes. *Landscape Ecology*, **31**, 301–315

605 Neumann, J.L., Griffiths, G.H., Foster, C.W. & Holloway, G.J. (2016) The heterogeneity of  
606 wooded-agricultural landscape mosaics influences woodland bird community assemblages.  
607 *Landscape Ecology*, **31**, 1833–1848.

608 Oliver, T., Roy, D.B., Hill, J.K., Brereton, T. & Thomas, C.D. (2010) Heterogeneous  
609 landscapes promote population stability. *Ecology Letters*, **13**, 473–484.

610 OS. (2010) Data from: Ordnance Survey MasterMap Download. Edina Digimap. Data  
611 obtained under licence. Available at:  
612 <http://digimap.edina.ac.uk/mastermapdownloader/Downloader>

613 OS. (2013) Data from: Ordnance Survey Historic mapping, Country Series 1846-1969. Edina  
614 Digimap. Data obtained under licence. Available at:  
615 <http://digimap.edina.ac.uk/mastermapdownloader/Downloader>.

616 Oxbrough, A., Irwin, S., Kelly, T.C. & O'Halloran, J. (2010) Ground-dwelling invertebrates  
617 in reforested conifer plantations. *Forest Ecology and Management*, **259**, 2111–2121.

618 Piessens, K. & Hermy, M. (2006) Does the heathland flora in north-western Belgium show an  
619 extinction debt? *Biological Conservation*, **132**, 382–394.

620 Piqueray, J., Bisteau, E., Cristofoli, S., Palm, R., Poschlod, P. & Mahy, G. (2011) Plant  
621 species extinction debt in a temperate biodiversity hotspot: Community, species and  
622 functional traits approaches. *Biological Conservation*, **144**, 1619–1629.

623 Rackham, O. (1986) *The History of the Countryside*. J.M. Dent, London.

624 Rackham, O. (2003) *Ancient Woodland: Its History, Vegetation and Uses in England. Second*  
625 *Edition*. Castlepoint Press, UK.

626 Radford, J.Q. & Bennett, A.F. (2007) The relative importance of landscape properties for  
627 woodland birds in agricultural environments. *Journal of Applied Ecology*, **44**, 737–747.

628 Rybicki, J. & Hanski, I. (2013) Species-area relationships and extinctions caused by habitat  
629 loss and fragmentation. *Ecology Letters*, **16**, 27–38.

630 Sang, A., Teder, T., Helm, A. & Partel, M. (2010) Indirect evidence for an extinction debt of  
631 grassland butterflies half century after habitat loss. *Biological Conservation*, **143**, 1405–1413.

632 Schweiger, O., Malfait, J.P., Van Wingerden, W. Hendrickx, F., Billeter, R., Speelmans M.,  
633 Augenstein, I., Aukema, B., Aviron, S., Bailey, D., Bukacek, R., Burel, F., Diekötter, T.,  
634 Dirksen, J., Frenzel, M., Herzog, F., Liira, J Roubolava, M. & Bugter, R. (2005) Quantifying  
635 the Impact of Environmental Factors on Arthropod Communities in Agricultural Landscapes  
636 across Organizational Levels and Spatial Scales. *Journal of Applied Ecology*, **42**, 1129–1139.

- 637 Spencer, J & Haworth, R. (2005) *Heathland on the Forestry Commission Estate in England*.  
638 Forestry Commission England, Bristol, UK.
- 639 Southall, H., Baily, B. & Aucott, P. (2007) *1930's Land utilisation mapping: an improved*  
640 *evidence-base for policy?* Science Report SC050031. Environment Agency, Bristol.
- 641 Taboada, A., Kotze, D.J. & Salgado, J.M. (2004) Carabid beetle occurrence at the edges of  
642 oak and beech forests in NW Spain. *European Journal of Entomology*, **101**, 555–563.
- 643 Ter Braak, C.J.F. & Šmilauer, P. (2012) *Canoco reference manual and user's guide: software*  
644 *for ordination*. Version 5.0. Microcomputer Power, Ithaca, USA.
- 645 Tilman, D., May, R.M., Lehman, C.L. & Nowak, M.A. (1994) Habitat destruction and the  
646 extinction debt. *Nature*, **371**, 65–66.
- 647 Vanbergen, A.J., Woodcock, B.A., Watt, A.D. & Nimela, J. (2005) Effect of Land-Use  
648 Heterogeneity on Carabid Communities at the Landscape Scale. *Ecography*, **28**, 3–16.
- 649 Vickery, J.A., Tallowin, J.R., Feber, R.E., Asteraki, E.J., Atkinson, P.W., Fuller, R.J. &  
650 Brown, V.K. (2001) The management of lowland neutral grasslands in Britain: effects of  
651 agricultural practices on birds and their food resources. *Journal of Applied Ecology*, **38**, 647–  
652 664.
- 653 Walker, K.J., Stevens, P.A., Stevens, D.P., Mountford, J.O., Manchester, S.J. & Pywell, R.F.  
654 (2004) The restoration and re-creation of species-rich lowland grassland on land formerly  
655 managed for intensive agriculture in the UK. *Biological Conservation*, **119**, 1–18.
- 656 Warren, M.S., Hill, J.K. & Thomas, J.A. (2001) Rapid responses of British butterflies to  
657 opposing forces of climate and habitat change. *Nature*, **414**, 65–68.

658 Watts, K., Eycott, A. E., Handley, P., Ray, D., Humphrey, J.D. & Quine, C.P. (2010)  
659 Targeting and evaluating biodiversity conservation action within fragmented landscapes: an  
660 approach based on focal generic species and least-cost networks. *Landscape Ecology*, **25**,  
661 1305–1318.

662 Wiezik, M., Svitok, M. & Dovciak, M. (2007) Conifer introductions decrease richness and  
663 alter composition of litter-dwelling beetles (Coleoptera) in Carpathian oak forests. *Forest*  
664 *Ecology and Management*, **247**, 61–71.

665

#### 666 **(A) DATA ACCESSIBILITY STATEMENT**

667 Requests for access to data used and analysed in this study can be made by emailing the  
668 corresponding author.

669

#### 670 **(A) BIOSKETCH**

671 The research team comprises individuals from UK academic and conservation research  
672 institutions with a broad range of expertise in landscape ecology and practical conservation  
673 across multiple taxonomic groups (<http://www.reading.ac.uk/cwac/>).

674 JLN and GHG conceptualised the study. JLN collected and analysed the data, GJH and AH  
675 assisted with carabid identification. JLN led the manuscript writing with input and editing  
676 provided by all authors.



**Table 1:** Summary of landscape composition and landscape configuration variables used to represent the contemporary and historical landscape heterogeneity in 36 study tetrads. Table also details additional constraining variables considered in the analyses.

Main set	Sub set	Broad Habitat variables
<b>Landscape composition</b>	Woodland land-use	Amount (ha) of broadleaf woodland (“Woodland”)
		Amount (ha) of coniferous plantation (“Coniferous”)
	Agricultural land-use	Amount (ha) of arable land (“Arable”)
		Amount (ha) of improved grassland (“Improved grassland”)
	Semi-natural land-use	Amount (ha) of semi-natural grasslands (“Grasslands”)
		Amount (ha) of inland water (“Water”)
		Amount (ha) of heathland and scrub (“Heath and scrub”)
	Urban land-use	Amount (ha) of suburban and urban (“Urban”)
<b>Landscape configuration</b>	Woodland metrics	Total number of woodland patches (“WP”)
		Mean area (ha) of woodland patches (“MPA”)
		Total length (km) of woodland edge (“WE”)
		Perimeter: Area ratio of the sample woodland (“PAR”)
	Semi-natural habitat	Total number of semi-natural grassland patches (“NPG”)
	metrics	Mean area (ha) of semi-natural grassland patches (“MPG”)
		Total number of heathland and scrub patches (“NPH”)
		Mean area (ha) of heathland and scrub patches (“MPH”)
		Total length (km) of main roads and railways (“RD”)
<b>Constraining variables</b>	Sampling date	Date of first carabid collection after 7 days (fortnight midpoint)
	Spatial location	British National Grid coordinate (XY) at tetrad midpoint

Abbreviations in brackets represent variable identification code on analysis bi-plots

681 **Table 2:** Average change in the composition and configuration of Broad Habitats (BH) comparing between  
682 2007 (contemporary landscape) and the 1930's (historical landscape).

Landscape composition (BH)	Contemporary		Historical	
	Mean area	% cover of	Mean area	% cover of
	(ha)	tetrad	(ha)	tetrad
Arable land	155.7 ha	38.9%	94.0 ha	23.5%
Improved grassland	85.9 ha	21.5%	0 ha	0%
Broadleaf woodland	96.6 ha	24.2%	106.5 ha	26.6%
Coniferous plantation	14.2 ha	3.5%	0 ha	0%
Heath and scrub	1.7 ha	0.4%	32.8 ha	8.2%
Grasslands	14.4 ha	3.6%	155.2 ha	38.8%
Inland water	1.0 ha	0.2%	3.43 ha	0.9%
Suburban and urban	25.4 ha	6.3%	17.4 ha	4.3%

  

Landscape configuration (BH)	Contemporary	Historical
	Mean values	Mean values
Number woodland patches	19 patches	11 patches
Area woodland patches	6.2 ha	16.3 ha
Length woodland edge	19.8 km	11.3 km
Number grassland patches	5 patches	9 patches
Area grassland patches	3.0 ha	36.7 ha
Number heath /scrub patches	9 patches	2 patches
Area heath/scrub patches	0.2 ha	15.3 ha
Length of roads and railways	2.2 km	1.8 km

683

**Table 3:** Response of woodland carabid communities to contemporary and historical landscape composition and landscape configuration across 36 tetrads. Results show the key explanatory variables identified by interactive forward selection for each model, following a significant ( $p < 0.05$ ) global permutation test.

Landscape composition	Global significance test			Interactive selection		
	F	P	Var	Key variables	Var	p-value
Contemporary	1.3	0.009	29.7%	Heath & scrub	5.0%	0.073
				Arable	4.9%	0.015
				Grassland	4.2%	0.045
				Coniferous	3.9%	0.098
Historical	1.3	0.005	23.0%	Arable	5.9%	0.008
				Woodland	4.3%	0.031
Landscape configuration	Global significance test			Interactive selection		
	F	P	Var	Key variables	Var	p-value
Contemporary	1.3	0.064	32.1%	WE	4.8%	0.033
				MPA	4.2%	0.084
Historical	1.4	0.006	34.7%	MPG	4.8%	0.064
				MPA	4.8%	0.062
				WE	4.3%	0.045
				RD	3.8%	0.085

Var = total variation in carabid community composition explained by all the landscape variables (global significance test) and the total amount of variation explained by each individual variable (identified during forward interactive selection). Refer to Table 1 for landscape variable abbreviations. Significance levels determined by Monte-Carlo global permutation tests.

**Fig. 1:** Location of the 36 2 x 2 km study tetrads in central southern England and a thematic representation of landscape change, comparing the historical and contemporary landscapes for one study tetrad.

**Fig. 2:** Partial Canonical Correspondence Analysis (pCCA) bi-plot illustrating the response of carabid communities to contemporary landscape composition variables. Key explanatory variables identified by partial Interactive Forward Selection (pIFS). For legibility, bi-plot displays the 25 species that are well described by the first two ordination axes (which together explain 11.6% of the total variation) and are shown using bi-plot scaling. Refer to Table 1 for variable abbreviations and Table S3 for full species names.

**Fig. 3:** Partial Canonical Correspondence Analysis (pCCA) bi-plot illustrating the response of carabid communities to historical landscape composition variables. Key explanatory variables identified by partial Interactive Forward Selection (pIFS). For legibility, bi-plot displays the 25 species that are well described by the first two ordination axes (which together explain 10.2% of the total variation) and are shown using bi-plot scaling. Refer to Table 1 for variable abbreviations and Table S3 for full species names.

**Fig. 4:** Partial Canonical Correspondence Analysis (pCCA) bi-plot illustrating the response of carabid communities to contemporary landscape configuration variables. Key explanatory variables identified by partial Interactive Forward Selection (pIFS). For legibility, bi-plot displays the 25 species that are well described by the first two ordination axes (which together explain 9.0% of the total variation) and are shown using bi-plot scaling. Refer to Table 1 for variable abbreviations and Table S3 for full species names.

**Fig. 5:** Partial Canonical Correspondence Analysis (pCCA) bi-plot illustrating the response of carabid communities to historical landscape configuration variables. Key explanatory variables identified by partial Interactive Forward Selection (pIFS). For legibility, bi-plot displays the 25 species that are well described by the first two ordination axes (which together explain 11.0% of the total variation) and are shown using bi-plot scaling. Refer to Table 1 for variable abbreviations and Table S3 for full species names.

713 **Supporting Information**

714 Additional Supporting Information may be found in the online version of this article:

715 **Table S1:** Creation of Broad Habitat categories derived from LCM2007 and OSMM data.

716 **Table S2:** Pearson correlation matrices for landscape variables in each year and between time periods.

717 **Table S3:** Record of carabid species, bi-plot codes and species characteristics.